

**Scientific note****The continuing debate on the history of the Amazonian rain forest**

by

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A comment on "Climatic forcing of evolution in Amazonia during the Cenozoic: on the refuge theory of biotic differentiation" by HAFFER & PRANCE (2001), and "A paradigm to be discarded: Geological and paleoecological data falsify the HAFFER and PRANCE refuge hypothesis of Amazonian speciation" by COLINVAUX et al. (2001).

Although the tropical rainforest is among the most complex and species-rich ecosystems in the world and receives the most attention from the public for many different reasons, it has hardly any environmental history. As a consequence, there is much speculation in the literature. Several decades ago, HAFFER (1969) presented an hypothesis of such elegance that all disciplines began to fit their sparse data into this framework. Modern distributional patterns and phylogenetic data on many floral and faunal taxonomic groups have been evaluated against HAFFER's hypothesis, creating an ever-increasing volume of circumstantial evidence in its support. Curiously, however, little effort has been expended to increase the direct, pollen-based evidence to test the model.

The most convincing evidence to reconstruct the ice-age environment has to come from a network of well-dated pollen records that reaches as far back as the Last Glacial Maximum (LGM), but only a handful of researchers has chosen to work in Amazonia. Access to many parts of the region remains difficult and bringing back sediment cores to laboratories is even more difficult. Projects for collecting sediment cores from Amazonian lakes deserve the same level of support commonly available for marine and ice-core studies and national funding agencies should assume their share of responsibility for improving the quality of the research. Additional support from geomorphological and geological studies is welcome, but the disagreement in both papers over the signifi-

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\*Dedicated to Prof. Dr. Harald Sioli on the occasion of his 90th anniversary.



cance of poorly dated features, such as "fossil dunes" and "stone lines", makes it clear that we have to rely primarily on well-dated pollen-based evidence. Contrary to the opinions of HAFFER & PRANCE (2001), all undated material should be discarded.

But the interpretation of palynological data from the Amazon basin is also not without debate. COLINVAUX et al. (2001) consider the periods with open vegetation in the Carajás pollen record as evidence of increased "altitudinal savanna" correlated with lower water level in the lakes on the plateau-like highlands. Such a vegetation change could have been limited to the inselberg area, however, and if so, there would have been no change in the biome of southeastern Amazonia as suggested by ABSY et al. (1991) and HOOGHMSTRA & VAN DER HAMMEN (1998). As Carajás seems to be a key site in the ongoing discussion, we badly need the results of additional cores and a better understanding of how representative the change in the vegetation on the plateau was for the area at large.

It must be admitted that the sites with last-glacial pollen-based evidence for drier types of vegetation – Carajás, Rondônia, and Guyana – are all located close to the margins of the present-day rain forest. If the impact of the precession-forced migration of the caloric equator on the position of the belt of tropical rains (ITCZ) is as strong and straightforward as suggested by MARTIN et al. (1997), these pollen records can possibly be taken as additional support for their paper. Very recent Holocene pollen records do show competition between wet (gallery) forest and savanna at the southern border (Bolivia: MAYLE et al. 2000) and the northern border (Colombia: BEHLING & HOOGHMSTRA 2000; WILLE et al. 2002) of the rain forest. Thus, Carajás, Rondônia, and Guyana can be considered as reflecting precession-forced change, but more far-reaching conclusions are premature. Evidence for replacement of rain forest by savanna-like vegetation in the central Amazon basin is lacking and it is not appropriate to draw the conclusion that pleases COLINVAUX et al. (2001) until more pollen records become available.

The increased representation in pollen spectra of *Podocarpus* (possibly pointing to cooler conditions) and *Clusia* (possibly pointing to lower atmospheric CO<sub>2</sub> concentration, with different floral composition of the forest as a consequence) in the glacial Amazon provides the first evidence for different forest composition in response to different climatic parameters, but pollen spectra of this age are few. More systematic studies of the modern distributions of *Podocarpus*, *Clusia*, and other major Amazonian lowland taxa, and of the glacial forest composition are necessary before such indications can be confidently interpreted. DUIVENVOORDEN & LIPS (1993) have shown that small families in particular seem to offer good opportunities for inferring specific environmental conditions. It is to be hoped that pollen morphologists will use such studies more frequently as a guide for selecting the next taxonomic groups for developing pollen morphological keys.

Difficult conditions for exploration in the Amazon basin make it attractive to look offshore, where most of the sediments from the basin are deposited. However, marine palynology is never a substitute for raising lake cores inland. The monotonous pollen records in the Amazon fan cores spanning the Holocene and much of the last ice age are considered by several authors to be evidence for stable conditions in the basin. However, this line of reasoning is weak (HOOGHMSTRA & VAN DER HAMMEN 1998) and much greater understanding of the significance of the pollen signal in river and fan sediments is needed. Meanwhile, the decisive conclusions in the literature are

premature.

The pollen diagrams from six lakes in the Colombian savanna show that the greater their isolation from the surrounding open savanna by gallery forest, the less the percentage of grass pollen in their sediments (BERRIO et al. 2000, 2002). If COLINVAUX et al. (2001) want to invalidate this conclusion, it is preferable to sample another six savanna lakes (as well as savanna rivers), rather than try to do so using data from European lakes, models, and theoretical considerations.

HAFFER & PRANCE (2001) cite the effect of MILANKOVITCH cycles on the rain forest during the Quaternary and Tertiary to substantiate the dynamic character of the rain forest. These very theoretical ideas have also been ventilated by DYESIUS & JANSSEN (2000). Although precession forcing has an impact on the rain forest in marginal areas, as shown in the above-mentioned Holocene records, the introduction of MILANKOVITCH forcing into the debate is not helpful in validating the forest refugia hypothesis. It is more relevant to obtain additional pollen records from strategically located sites.

It is regrettable that so elegant a hypothesis has become a divisive element in the paleoecological community. Most of the energy has been devoted to obtaining indirect support, which is an inadequate procedure. The paleoecological community would be better served by creating a network of lake records that reach minimally back to the last glacial maximum, but preferably longer, for which COLINVAUX's Pata record is a current benchmark. Lacking this, many of the conclusions from both "schools" are premature and decisive validation or falsification of HAFFER's hypothesis is impossible.

During the next decade, we should focus on activities that substantially improve the quality of Amazonian pollen-based climatic archives. These should include: (1) elaborating pollen morphological keys for those taxonomic groups most indicative of climatic variables; (2) improving understanding of the modern distributions of Amazonian taxa and their ecological envelope ("climate space"); (3) improving pollen-based recognition of the suite of forest types between wet forest, semi-deciduous forest, and dry forest, as well as the various types of forested savanna and open savanna, and (4) creating a network of pollen-based climatic records, amongst others along gradients of annual precipitation and increasing seasonality.

For HAFFER & PRANCE (2001), the refuge theory remains a working model. They have clearly eliminated misconceptions in the recent literature. COLINVAUX et al. put the refuge theory in its grave before verifying whether the patient is really dead and demonstrate their conviction by the increasingly resolute titles of their recent papers (compare COLINVAUX et al. 2000, 2001). In my opinion, the available evidence is far too inadequate to make any well-documented decision. The presence of refugia during the LGM can only be demonstrated on the basis of direct palynological evidence from Amazonian cores, not on the basis of modern distributional patterns or marine palynological evidence. I would not be surprised if we have to conclude in a decade or so that most of central Amazonia was permanently covered with various types of forest during the last glacial-interglacial cycle, ranging from super-wet to semi-deciduous and dry forest, and that changes between various types of forest and open savanna-like landscapes were mainly restricted to the northern and southern borders of the present rain forest area. Whether the LGM dry (forest) corridor in eastern Amazonia, which is clearly shown on the vegetation maps of some climatic models, did indeed exist can be



established by obtaining only a few new pollen records. Finally, comparisons between paleodata and models are needed to explore the environmental dynamics that drove the Amazonian dry/moist forest transitions from the last glacial maximum until the present day.

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